

ner keine Beziehung zwischen der Inzuchtdepression in der Höhe und der Selbstfertilität der Elternbäume oder ersterer und der Höhenlage der Herkunft dieser Bäume.

Das Verhalten von Sämlingen aus Windbestäubung wurde in den Vergleich einbezogen. Dabei zeigte sich, daß die Umwelt in den Isolierungstüten das Samengewicht und die Sämlingsgröße beeinflußt hatte. Beides stieg bei der Douglasie an und nahm bei der Ponderosa ab. Die Häufigkeit von Selbstungssämlingen in einer frei abgeblühten Population wird bei Douglasie auf 6,4% und bei der Ponderosa auf 11,3% geschätzt. Dies ergibt sich, wenn das Sterblichkeitsprozent, das durch Majorgen-Effekte hervorgerufen wird, zugrunde gelegt wird. Eine Schätzung bei Wuchsdaten konnte wegen der Auswirkungen der Samengewichte nicht durchgeführt werden. Bei künstlichen Populationen aus Selbstungs- und Fremdbestäubungs-Sämlingen wurde der Effekt von Baumschulauslese auf die Entfernung von Selbstungssämlingen beschrieben.

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The Inheritance of Heartwood Formation in *Pinus radiata* D. Don.

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Introduction

The modifications to wood anatomy associated with heartwood formation are important in many aspects of utilisation, both for sawn timber and pulp and paper. These changes result in a greatly increased resistance to the movement of liquids from one cell to another so that seasoning difficulties are increased and the material is less readily penetrated by preservatives and pulping liquors. In addition, there is evidence that the heartwood of coniferous trees almost invariably contains more resin than the sapwood, and the difference is particularly marked in the pines (MUTTON 1962; KEITH 1969). The presence of resins can also influence the usefulness of the raw material, such as for example by adversely affecting the paper-making qualities.

Heartwood development begins some distance above ground level in pines (LIESE 1936; TRENDLENBURG 1939; PAUL 1952), and then extends both towards the crown and the butt. The age of its inception in *P. radiata* was noted by HARRIS (1954) as approximately 14 years from time of planting and the average rate of transformation of sapwood to heartwood was reported by NICHOLLS and DADSWELL (1965)

as approximately 0.5 growth rings per year. There is little published information on the inheritance of heartwood formation and the two available estimates of heritability were derived from *P. radiata* clonal material (NICHOLLS 1965a). As it is not practical to investigate the variation in age at which heartwood begins to form, these estimates were based on the area proportion of heartwood.

There is a need to extend these preliminary estimates by work on both clonal and sexually reproduced material. Results of some further studies are reported below.

Materials

The trees for examination originated at three different localities.

Group 1. Material previously sampled in 1960 to obtain heritability estimates for the proportion of heartwood by NICHOLLS (1965a) and growing in a *P. radiata* clonal trial established in 1939 at a spacing of 2.4 m X 2.4 m at Blue Range plantation in the Australian Capital Territory. The plantation is 25 km west of Canberra at an elevation of 780 m. The site slopes gently with an eastern aspect and soil is derived from Ordovician sediment. Mean annual rainfall is 1015 mm. Thirteen clones were sampled by selecting the first, middle and last trees of the row com-

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prising the clone. Only vertical trees were chosen.

Group 2. Experimental material previously used to obtain heritability estimates for other wood characteristics by NICHOLLS (1965 b) and growing in a clonal plantation of *P. radiata* established in 1940 at Mt. Burr, South Australia. The clones were propagated from cuttings and planted in adjacent rows without replication at a spacing of 2.8 m × 2.1 m. The site is without appreciable slope, of practically uniform quality and located on a transitional volcanic soil described as a coarse, sandy, valley type.

From each of 19 clones, after excluding trees of low vigour, 3 trees were chosen at random.

Group 3. Specimens were obtained from *P. radiata* trees previously sampled to obtain heritability estimates for other wood characteristics (NICHOLLS *et al.* 1964) and growing in a progeny trial established at Kowen plantation in the Australian Capital Territory in 1952. The plantation is 14 km east of Canberra at an elevation of 750 m. The gently undulating site is on shallow soil derived from Ordovician sediment and was deeply ripped at planting time.

The trial contains open-pollinated progenies from 33 trees previously selected for vigour, form and branching characteristics. In each of five blocks the 33 progeny groups were randomly allocated to 33 plots or rows, the progeny from one parent being confined to a single twenty-tree row in each block. Spacing was 2.4 m × 2.4 m. The first three trees in every plot were sampled making a total of 495 trees in all.

Experimental Procedures

Wood specimens were collected from the selected trees as follows: —

Group 1. Increment cores 5 mm in diameter extending from bark to bark and including the pith were taken in November 1972 adjacent to the previous sampling heights of 1.2 m and 4.6 m. Generally the interval between the old and new sampling positions was about 15 cm to avoid any modified wood resulting from the extraction of the 1960 cores. In two cases trees had died and could not be resampled.

Group 2. Wood cores 35 mm in diameter extending from bark to bark and including the pith were taken at a nominal breast high position in November 1964. Individual sampling heights were adjusted so that all specimens exhibited 22 complete growth rings.

Group 3. Increment cores 5 mm in diameter extending from bark to bark and including the pith were collected between December 1972 and March 1973 adjacent to the previous sampling positions, that is, a nominal breast high position, taking the same precautions outlined for the Group 1 specimens. About 5 per cent of the full complement of 495 specimens could not be obtained because of losses in the plots due to deaths and fellings for other work.

All cores were examined as soon as possible after receipt at the laboratory. The heartwood-sapwood boundary was identified, and the radial extent of the heartwood and the pith to bark distance was recorded for each radius of each specimen. In each case the extent of the heartwood for the two radii were averaged and used to express the heartwood area as a proportion of the total cross-sectional area. The diazotized benzidine stain of KOCH and KRIEG (1938) was used to distinguish this boundary in the 5 mm cores. For the larger Group 2 cores a thin transverse strip was cut from each and viewed in the green state against a

strong white light to determine the heartwood-sapwood boundary.

Data were tabulated separately for each set of specimens and submitted to statistical analyses to separate components of variance. For the clonal material (Groups 1 and 2) heritability in its broad sense (gross heritability) may be estimated as the ratio of the between-clone variance to phenotypic variance, subject to two provisos — that the amount of environmental variance confounded with the between-clone variance (because of the un-randomised clonal layout) is relatively small, and secondly that any real differences between clones are genetic ones, rather than partly or wholly the expression of common physiological or morphological conditions between ramets within each clone at the time of cloning (“c” effects, LIBBY 1962; SHELBOURNE 1969). With regard to the first qualification, it is the authors’ belief because of the layout of Group 1 and Group 2 trees that little of the between-clone variance is of environmental origin. In the second matter, the “c” effects need only be excluded from the heritability estimate if the figures are to be used as a guide to the likely genetic gain in sexually reproduced material. The variation in heartwood content was separated by analyses of variance into within-clones and between-clones components and gross heritability was estimated as:

$$h^2 = \frac{\text{between-clone variance}}{\text{between-clone variance} + \text{within-clone variance}}$$

For the Group 3 progeny which were propagated by sexual means, non-additive genetic variance resulting from dominance and epistasis cannot be expressed so that heritability is used in the narrow sense. Variance components were estimated from analyses of variance of the form used in the previous study for this material and reported by NICHOLLS *et al.* (1964). The estimate of narrow sense heritability was given as:

$$h^2 = \frac{4 \sigma_p^2}{\sigma_p^2 + \sigma_w^2 + \sigma_{hp}^2}$$

where environmental variance is defined as $\sigma_w^2 + \sigma_{hp}^2$, the genetic component, is σ_p^2 , and the relationship between members of a progeny groups is assumed to be half-sib. However there is a probability that a proportion of the within-group relationship will be full sib and the additive genetic variance will be between $2 \cdot \sigma_p^2$ and $4 \cdot \sigma_p^2$ (NICHOLLS *et al.* 1964) so that the heritability estimate will be slightly less than that given by the above-mentioned relationship.

Results and Discussion

The mean squares, heritability estimates and their standard errors for the clonal material from the Blue Range plantation are shown in *Table 1*. There is no sensible difference, at least at the 1.2 m height, between the values derived from the 1960 samplings and those from specimens obtained in 1972. That is, the expression of the genetic and environmental factors that influence the transformation of sapwood to heartwood has remained relatively constant during the 12 year interval. During this period however, the area proportion of heartwood in the stem cross-section increased on the average from 0.056 to 0.230 at the 1.2 m level and from 0.068 to 0.260 at the 4.6 m height.

The results from the analysis of the clonal material from Mt. Burr are recorded in *Table 2*. The decreased standard error and increased significance of the heritability estimate reflect the increased number of observations in this study compared to those derived from the Group 1 investigation.

Table 1. — Mean squares and heritabilities for the area proportion of heartwood at heights of 1.2 m and 4.6 m in *P. radiata* clones from the Blue Range plantation.

Year of sampling	Specimen height (m)	Mean squares		Degrees of freedom		Heritability	S.E.
		B.C.	W.C.	B.C.	W.C.		
1960	1.2	13.24*	4.807	12	26	0.37	0.18
	4.6	21.02*	7.777	12	26	0.36	0.18
1960 †	1.2	12.86*	4.934	12	24	0.37	0.19
	4.6	22.08*	7.420	12	24	0.41	0.19
1972	1.2	12.54*	5.156	12	24	0.34	0.19
	4.6	11.18 ⁿ	5.149	12	24	0.30	0.20

B.C. — between clones

W.C. — within clones

* — significant at 5 per cent level

ⁿ — not significant

† — based on only those trees sampled in 1972.

Table 2. — Mean squares and heritabilities for the area proportion of heartwood at breast height in *P. radiata* clones from Mt. Burr, South Australia.

Mean squares		Heritability	S.E.
B.C.	W.C.		
82.12**	23.91	0.45	0.14

B.C. — between clones — 18 degrees of freedom.

W.C. — within clones — 38 degrees of freedom.

** — significant at 1 per cent level.

It is gratifying to have confirmation of the original estimates (NICHOLLS 1965 a) from results based on trees of differing genotype and grown under very different environmental conditions. It is interesting to note that differences due to the two techniques used in determining the heartwood-sapwood boundary, that is, staining for Group 1 and viewing the green cross-sections against a strong light for Group 2, are not apparent in the results.

The estimate of narrow sense heritability for the progeny material from the Kowen plantation is shown in Table 3. The value of 0.20 is, as a rule, of the same order as the narrow sense estimates published for the other wood characteristics under investigation in the previous study using these experimental trees (NICHOLLS *et al.* 1964).

The estimates from the three groups generally support one another and suggest that there is some prospect of modifying the incidence of heartwood by selection. Strictly speaking, the present results apply only to the three plantations but there is sufficient diversity between the groups to justify extrapolation to other *P. radiata* populations in south-east Australia.

A prediction of the expected gain has been calculated for the group 3 material, based on the collection of open-pollinated seed from selected trees, using the expression suggested by SHELBORNE (1969); that is

Table 3. — Variance components and estimate of heritability for the area proportion of heartwood at breast height in *P. radiata* from Kowen plantation.

Variance Components	Heritability	S.E.
σ_p^2	3.4127	
σ_{bp}^2	9.5824	
σ_w^2	54.8517	
	67.8468	
	0.20	0.14

$$\Delta G = i \cdot \frac{1}{2} \cdot \frac{\sigma_A^2}{\sigma_1} \cdot \frac{1}{\bar{x}}$$

where ΔG is the expected gain, σ_A^2 is the additive genetic variance ($4\sigma_p^2$), σ_1 is the square root of the total phenotypic variance ($\sigma_p^2 + \sigma_{bp}^2 + \sigma_w^2$) and \bar{x} is the population mean proportion of heartwood = 13 per cent. Two cases are considered, viz. selection of the lowest heartwood tree, out of 10 ($i = 1.75$), and out of 100 ($i = 2.66$) (SHELBORNE 1969), in both cases within a forest area corresponding to the replicate size used in the experiment. Saving one in 10 results in 11% gain, and saving one in 100 in 17% gain in the resulting offspring with respect to the unselected population mean. That is, the resulting mean proportion of heartwood in the offspring, will be 11.6 per cent and 10.8 per cent respectively.

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Summary

Estimates of heritability for the area proportion of heartwood in *Pinus radiata* are reported. Results based on clonal material from the Australian Capital Territory were similar to those obtained from the same trees 12 years previously and agreed closely with values derived from clonal material from South Australia. An estimate of narrow sense heritability is also reported from progeny trial samplings.

Key words: Heartwood, heritability, *Pinus radiata*.

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Effect of Seed Origin on Coppice Regeneration in *Eucalyptus camaldulensis* Dehn.*)

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Introduction

Eucalyptus camaldulensis DEHN. (*E. rostrata* SCHLECHT.) is one of the most widely grown eucalypts outside Australia. Its plantations are commonly managed as coppice; however, only limited information is available on the dynamics of coppice formation and growth and on its relation to environmental factors and tree size prior to cutting (CIANCIO and MORANDINI, 1971; JACOBS, 1955; KARSCHON, 1972).

Since ecotypic variation is known to occur in the species (KARSCHON, 1971, 1974), possible differences in the ability to coppice and in growth rate could be of practical interest when introducing locally better-adapted seed sources and evaluating alternative selection strategies (BURROWS, 1970). Investigations along these lines are still lacking.

Accordingly, the objectives of the present research were (a) to investigate the annual course and rate of coppice regeneration and its relation to tree size before cutting; and (b) to determine differences in coppice regeneration between progenies from different seed sources.

Materials and Methods

The investigation was conducted in an experimental plantation of *E. camaldulensis* approximately 6.5 years old at Ilanot (32° 18' N, 34° 54' E). The original layout was a

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split-plot design to test the effect of presence of lignotubers in the planting stock on tree growth, but growth rate was found to be not affected by the type of plants used (KARSCHON, 1971). Therefore, the sub-plots could be neglected and the coppice trial was analyzed as a randomized-block design with four progenies from bulk provenance collections (Table 1) and four replications, each plot consisting of eight trees spaced 3 × 3 m apart.

After measuring the height, girth at breast height (B.H.), and girth at 20 cm above ground, the trees were cut at about 10–15 cm above ground on 2 October 1972. At one-month intervals, counts were made of the number of sprouting stumps and of the number of sprouts per stump, and measurements were taken of the tallest shoot of each stump.

On 3 October 1973 the shoots were thinned according to current practice, leaving 1–3 shoots per stump. The fresh weight of the cut shoots was determined for each stump, to estimate the biomass, since in preliminary trials no statistically significant differences in moisture content were found between progenies (C. GRUNWALD, unpublished data).

Evaporation from a screened U. S. Weather Bureau Class A pan was 1,482 mm during the 12-month period following the cutting (Fig. 1D). Rainfall in 1972/73 was well below the yearly average of 603 mm and amounted to only 410 mm; the first and last effective rains were in the first week of December and of March, respectively.

Table 1. — Means of tree sizes prior to cutting (2 Oct. 1972) and of rates of coppice regeneration (3 Oct. 1973) in four progenies from Australia.

Progeny No.	Provenances	Latitude S	Longitude E	Before cutting			Coppice		
				Height m	Girth at B.H. cm	Girth at 20 cm cm	Maximum height m	Number of shoots	Biomass* kg
6788	Alice Springs, N. T.	23° 38'	133° 35'	6.33	14.6	21.3	1.66	19.9	1.035
6869	Katherine, N. T.	14° 25'	132° 15'	7.78	18.9	28.3	2.25	16.0	0.977
6949	N of Hughenden, Qld.	20° 43'	144° 21'	8.34	19.8	28.9	2.27	20.1	1.483
6953	Petford, Qld.	17° 20'	144° 57'	9.77	22.2	31.4	2.86	23.5	1.755
			S. E.	0.49	1.6	2.2	0.10	3.6	0.274

*) Fresh weight, excluding 1–3 shoots per stump left after thinning.